

***Schilbetrematoides pseudodactylogyrus* gen. et sp. n.**
(Monogenoidea, Dactylogyridae, Ancyrocephalinae) from the
Gills of *Schilbe intermedius* (Siluriformes, Schilbeidae)
in Togo, Africa

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ABSTRACT: *Schilbetrematoides pseudodactylogyrus* sp. n. (Dactylogyridae, Ancyrocephalinae) is described from the gills of *Schilbe intermedius* Rüppell, 1832, Siluriformes, Schilbeidae, in Togo. *Schilbetrematoides* gen. n. is proposed for this species and is characterized, in part, by large, subspherical eye granules; intercecal, overlapping gonads (testis dorsal); a constriction of the vas deferens at its union with the seminal vesicle; dorsal anchors; a ventral pair of 4A's lying near the ends of a simple (vestigial?) ventral bar; a highly modified dorsal bar; 14 hooks in 7 pairs with slender shanks and protruding thumbs.

KEY WORDS: Togo, Africa, Monogenoidea, Dactylogyridae, Ancyrocephalinae, *Schilbetrematoides* gen. n., *Schilbetrematoides pseudodactylogyrus* sp. n., *Schilbe mystus*, *Schilbe intermedius*.

During the relatively short period when Dr. I. Paperna worked on the freshwater Dactylogyridae from Africa, he proposed 13 of the 23 genera currently accommodating Ethiopian species (see Euzet and Dossou, 1976, and Paperna, 1979). Together, these genera appear to represent a well-defined picture of the freshwater dactylogyrid fauna of Africa's freshwater fishes. Indeed, since 1979, only *Paraquadiacanthus* Ergens, 1988 (= *Quadiacanthoides* Kritsky and Kulo, 1988; see Kritsky, 1990), and *Insulacleidus* Rakotofiringa and Euzet, 1983, have been proposed to accommodate African species. Similarly, our collections from Togo have not resulted in the identification of many new generic taxa. In the present paper, however, a new genus is erected for an unusual worm from the gills of a siluriform, *Schilbe intermedius* Rüppel, 1832 (Schilbeidae), from Togo. Although apparently sister taxon to *Schilbetrema* Paperna and Thurston, 1968 (Ancyrocephalinae), the new genus is characterized by many features of the Dactylogyriinae.

Materials and Methods

Fish hosts, *Schilbe intermedius*, were collected from the Mono River near Kolokopé, Togo, during 1985–1989. Methods for collection, preservation, mounting, and illustration of helminths were as described by Kritsky et al. (1987). Measurements, all in micrometers, were made with a filar micrometer according to the procedures of Mizelle and Klucka (1953), except that cirral length was an approximation obtained by using a calibrated Minerva curvimeter on camera lucida drawings; average measurements are followed by rang-

es and the number (*N*) of specimens measured in parentheses. Type specimens were deposited in the helminthological collections of the U.S. National Museum (USNM), USDA, ARS, Agricultural Research Center-East, Beltsville, Maryland; the University of Nebraska State Museum (HWM), University of Nebraska, Lincoln, Nebraska; the Musée Royal de l'Afrique Centrale (MRAC), B-1980 Tervuren, Belgium; and the British Museum (Natural History) (BM[NH]), London, U.K., as indicated in the description. A specimen of the host, *Schilbe intermedius* Rüppel, was deposited in the American Museum of Natural History, New York, as AMNH 57312.

Schilbetrematoides gen. n.

DIAGNOSIS: Dactylogyridae, Ancyrocephalinae. Body divisible into cephalic region, trunk, peduncle, haptor. Tegument thin, smooth. Two bilateral, 2 terminal cephalic lobes; head organs present; cephalic glands unicellular, comprising 2 bilateral groups posterolateral to pharynx. Eyes present, generally compact; granules large, subspherical. Mouth subterminal, midventral; pharynx, esophagus present; intestinal ceca 2, confluent posterior to gonads. Gonads intercecal, overlapping; testis dorsal to ovary. Vas deferens looping left intestinal cecum, constricting at union with seminal vesicle; seminal vesicle fusiform, lying parallel to left intestinal cecum; distal vas deferens slightly dilated (secondary seminal vesicle?), delicate; single prostatic reservoir closely associated with cirral base. Copulatory complex comprising proximally articulated cirrus, accessory piece; cirrus a loose clockwise coil (see Kritsky et al., 1985); accessory piece comprising proximal articulating rod, distal complex with

grooved cirral guide. Oviduct short; uterus delicate; vagina dextral, opening near body midlength; seminal receptacle ventral to anterior end of ovary. Haptor armed with dorsal pair of anchors; ventral pair of 4A's lying near ends of simple ventral bar; dorsal, ventral bars; 14 (7 pairs) hooks with ancyrocephaline distribution (Mizelle, 1936; see Mizelle and Price, 1963); dorsal anchor filaments present. Hooks with slender shanks, protruding thumb.

TYPE SPECIES, HOST, AND LOCALITY: *Schilbetrematoides pseudodactylogyrus* gen. et sp. n., from *Schilbe intermedius* Rüppel, Mono River near Kolokopé, Togo.

ETYMOLOGY: The generic name indicates the apparent close relationship of this taxon to *Schilbetrema* Paperna and Thurston, 1968.

Schilbetrematoides pseudodactylogyrus

gen. et sp. n.

(Figs. 1–9)

DESCRIPTION: Body 388 (240 [contracted]–548; $N = 8$) long, fusiform; greatest width 79 (62–109 [contracted]; $N = 8$) in posterior trunk. Cephalic lobes, cephalic glands poorly differentiated. Eyes 4; posterior pair slightly larger, members of respective pairs equidistant; accessory granules uncommon in cephalic, anterior trunk regions. Pharynx spherical, 22 (16–25; $N = 8$) in diameter; esophagus short. Peduncle broad; haptor subhexagonal, 64 (56–78; $N = 5$) wide, 79 (57–89; $N = 7$) long. Dorsal anchor 62 (56–70; $N = 10$) long, with elongate superficial root having superficial pustule near midlength, short deep root, curved shaft, point; base width 26 (22–31; $N = 7$); anchor filament ancyrocephaline. Ventral 4A: 10–11 ($N = 3$) long, proximally expanded about $\frac{1}{2}$ total length. Ventral bar 29 (25–34; $N = 8$) long, rod-shaped, with irregular anterior margin. Dorsal bar 17 (15–24; $N = 5$) long, plate-like, with enlarged ends, large projection arising from anterior bar margin; projection complex, with 2 elbowlike bends, the last serving as guide for anchor points; length of most dorsal fold (anteroposterior measurement) 66 (60–70, $N = 7$). Hooks similar; each 16 (14–17; $N = 22$) long, with slightly depressed thumb, delicate point, shank; FH loop about 0.75 shank length. Cirrus a loose coil of less than 1 ring, frequently appearing J-shaped, cirral base with sclerotized margin; cirral length 48 (47–55; $N = 6$), ring diameter 12 (10–16, $N = 5$). Accessory piece 27 (24–31; $N = 4$) long, comprising proximal uni-

form connecting rod, distal sheath with several variable branches, 1 of which serving as cirral guide. Testis elongate ovate, 51 (42–61; $N = 3$) \times 23 (22–24; $N = 3$); constriction of vas deferens with external spiral filament; seminal vesicle with distinct wall, fusiform; distal vas deferens pyriform; prostatic reservoir saccate. Ovary bacilliform, 43 (40–45; $N = 4$) \times 20 (17–23; $N = 3$); vagina funnel-shaped, with distal loop opening into large central seminal receptacle; vitellaria dense throughout trunk, except absent in fields of reproductive organs.

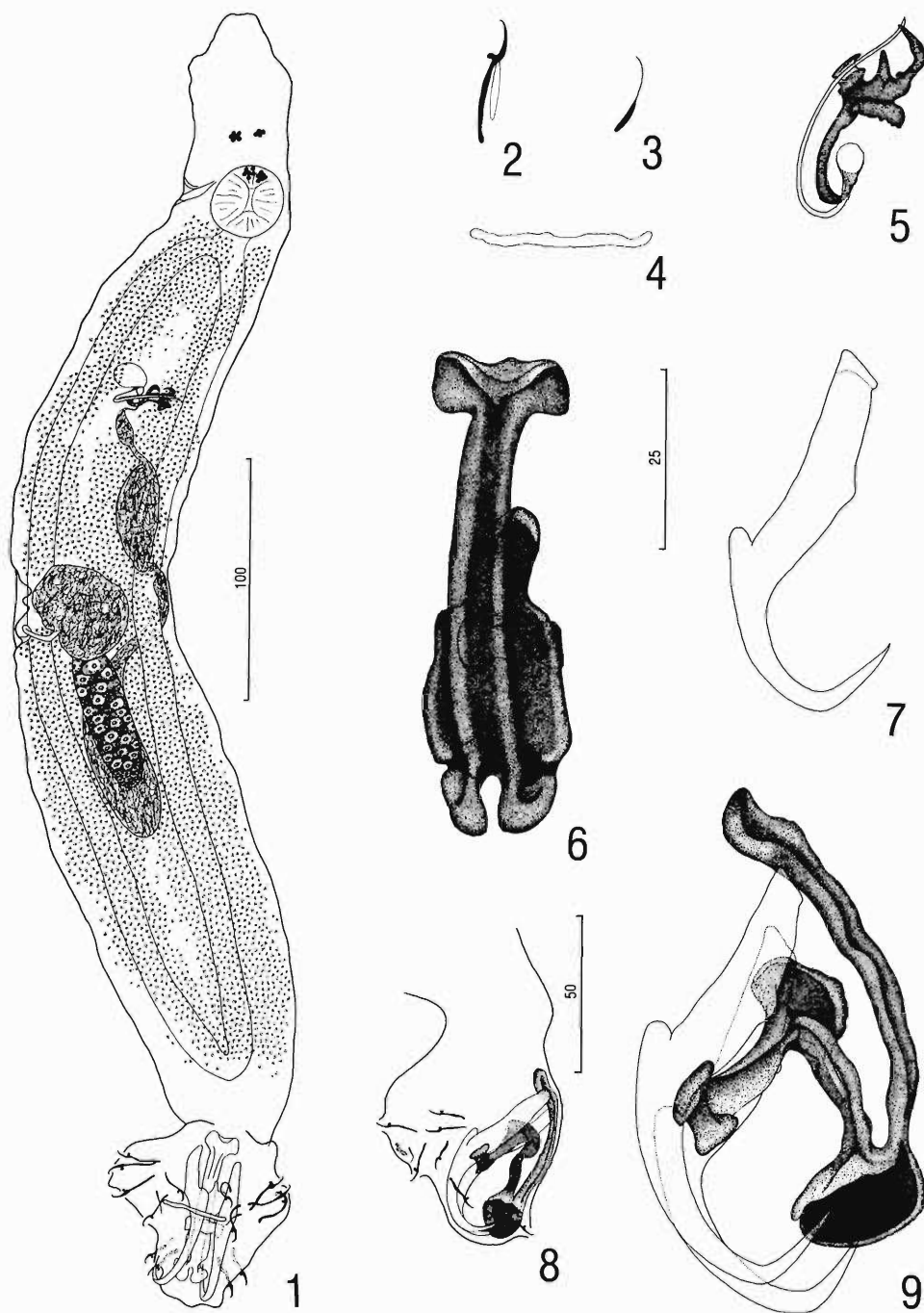
SPECIMENS STUDIED: Holotype, USNM 82093, 13 paratypes, USNM 82094, HWML 34290, MRAC 37.326, BM(NH) 1991.10.9.22.

ETYMOLOGY: The specific name refers to the superficial resemblance of the species to members of *Dactylogyrus* (Dactylogyridae, Dactylogyrinae).

Discussion

Our proposal of sister-group relationship of *Schilbetrematoides* and *Schilbetrema* Paperna and Thurston, 1968, is supported by several shared, apparently synapomorphic features. Among them, characteristics of the hooks, copulatory complex, eye granules, vagina, seminal vesicle, and distal vas deferens, and presence of a constriction of the vas deferens at its union with the seminal vesicle, appear to be the most significant (see Kritsky and Kulo, 1992). Basic features of the reproductive system of members of both genera are identical. However, these genera are presently differentiated primarily on haptor structure. Although some components are highly modified, the distribution of haptor sclerites in *Schilbetrema* spp. is typically ancyrocephaline, i.e., dorsal and ventral anchor/bar complexes present. In *Schilbetrematoides*, species possess a haptor organization approaching that found in the Dactylogyrinae, i.e., dorsal anchor/bar complex present, ventral pair of 4A's present, ventral bar absent or vestigial.

Without totally discounting the possibility of dispersal of some dactylogyrine ancestor to a siluriform host and subsequent convergence of many morphologic features, occurrence of *Schilbetrematoides pseudodactylogyrus* on a schilbeid (Siluriformes) host further supports the sister-group relationship proposed herein. "Fahrenheit's Rule" states that the phylogeny of parasite groups usually directly corresponds to the natural relationships of their hosts (Eichler, 1948). Al-



Figures 1–9. *Schilbetrematoides pseudodactylogyrus* gen. et sp. n. 1. Ventral view of holotype. 2. Hook. 3. 4A. 4. Ventral bar. 5. Copulatory complex. 6. Dorsal bar (dorsal view). 7. Dorsal anchor. 8. Lateral view of haptor (only sinistral members of hook pairs shown). 9. Dorsal anchor/bar complex (lateral view). All drawings are to the 25- μ m scale, except Figures 1 and 8 (100- μ m and 50- μ m scale, respectively).

though explanation of monogenoidean species on their hosts frequently requires instances of "host switching" (Boeger and Kritsky, 1989; Guégan and Agnès, 1991; Wheeler and Beverley-Burton, 1989; among others), Fahrenholz' Rule is likely reflected in relationships of *S. pseudodactylogyrus* and *Schilbetrema* spp., all of which are exclusively parasites of African schilbeids.

Bychowsky and Nagibina (1978) split the Ancyrocephalinae from the Dactylogyridae and elevated it to family status based primarily on haptor characteristics. These characters now appear to be insufficient to justify their action. Kritsky and Boeger (1989) provide evidence using cladistics that the Ancyrocephalidae (sensu Bychowsky and Nagibina, 1978) is paraphyletic and recommend that it be considered a junior synonym of the Dactylogyridae (sensu Yamaguti, 1963). Our finding of *Schilbetrematoides* and the characteristics it displays continue to cloud justification for the Ancyrocephalidae and, in addition, suggest probable polyphyly of the Dactylogyridae (Dactylogyridae sensu stricto of Bychowsky and Nagibina, 1978) as well.

Kritsky and Boeger (1989), among others, consider the presence of a single pair of anchors (dorsal) in the Dactylogyridae to represent a secondary loss of the ventral anchor pair. Taxa, based primarily on loss of structure(s), have a high risk of polyphyly because loss could have occurred many times with recognition of these independent occurrences difficult. In addition, structural loss in an evolutionary sense and particularly in parasites is potentially a more common occurrence than the development of new structures. As such, convergence, as shown by the absence of a structure, should be an expected outcome; proposal of new or the splitting of existing taxa based primarily on these characters, as engendered by Bychowsky and Nagibina, 1978, should be done conservatively.

Schilbetrematoides and perhaps some other genera (*Nanotrema* Paperna, 1969, *Trinidactylus* Hanek, Molnar, and Fernando, 1974, *Curvianchoratus* Hanek, Molnar, and Fernando, 1974, and *Acolpenteron* Fischthal and Allison, 1940) whose members occur on noncypriniform hosts and are considered by Gussev (1976, 1978) to comprise, in part, the Dactylogyridae sensu stricto, are potential groups in which loss of the ventral anchor pair may have occurred more than once throughout their evolutionary history. If

independent loss of the ventral anchor pair happened in one or more of these genera, the family (s.s.) is likely polyphyletic. Thus, loss of an anchor pair has a very limited value in defining this familial taxon. Secondary loss of an anchor pair(s) has already been assumed to have occurred independently outside the Dactylogyridae (s.s.) in *Trinigyris* Hanek, Molnar, and Fernando, 1974 (Ancyrocephalinae); *Pseudodactylogyrus* Gussev, 1965 (Pseudodactylogyridae); *Anonchopator* Mueller, 1938, and *Icelanonchopator* Leiby, Kritsky, and Peterson, 1972 (Pseudomurraytremaidae); and *Anacanthorus* Mizelle and Price, 1965, and *Anacanthoroides* Kritsky and Thatcher, 1976 (Anacanthorinae). In species of the ancyrocephaline genera, *Eutrianchoratus* Paperna, 1969, *Heteronchocleidus* Bychowsky, 1957, and *Trianchorus* Price and Berry, 1966, 1 member of the ventral anchor pair has been lost as a recognizable anchor but remains as a remnant resembling an early developing anchor.

Another feature that is used to place dactylogyrinid species lacking 1 or both of the anchor pairs in the Dactylogyridae is the presence of 4A's (Mizelle and Price, 1963) in the haptor (e.g., Gussev, 1978; Kritsky et al., 1978; Beverley-Burton, 1984). Circumstantial evidence, some of which is provided by *Schilbetrematoides pseudodactylogyrus*, continues to mount supporting the homology of the 4A with the respective lost anchor. This homology, implying each 4A to be an anchor vestige, was assumed by Kearn (1968) based on its relative position in the haptor and its temporal development in the larva and by Kritsky and Boeger (1989) based on parsimony. If *S. pseudodactylogyrus* is sister to *Schilbetrema* as proposed herein, the 4A's of the former are not homologues of those of the Dactylogyridae, and presence or absence of this feature can no longer be used to separate dactylogyrinids (sensu stricto) from so-called "ancyrocephalids." If 4A's are actually homologues of ventral anchors, they should be expected in any taxon within or without the Dactylogyridae showing incomplete loss of the haptor anchors.

We recognize that our proposal of the monotypic *Schilbetrematoides* gen. n. may result in paraphyly of *Schilbetrema*, because synapomorphic characters for the latter are not apparent. If *Schilbetrematoides pseudodactylogyrus* has a common ancestor (i.e., is sister species) with one or more of the *Schilbetrema* species infesting *Schilbe intermedius*, the new genus should be

considered a synonym of *Schilbetrema* with the new species a highly derived member. The spiral filament of the constriction of the vas deferens may be a character supporting this synonymy if its presence is the apomorphic state; a filamented constriction in *Schilbetrema* has only been observed in species infesting *Schilbe intermedius*. However, if the filament is synapomorphic for *Schilbetrema* + *Schilbetrematoides*, the character would not affect monophyly of the genera. Other characters, particularly associated with the highly modified haptor sclerites in *Schilbetrema*, may provide synapomorphies for this genus. An objective analysis will be required to determine phylogenetic support for *Schilbetrematoides*.

In order to avoid potential confusion, we add the following concerning recent proposals for change in the nomenclature of the host. Based on the International Code of Zoological Nomenclature and on the type specimen of *Silurus mystus* Linnaeus, 1758, De Vos and Skelton (1990) indicate that the epithet "*Schilbe mystus*" must be applied to schilbeids currently assigned to *Eutropius niloticus* (Rüppel, 1829). As a result, these authors indicate that *Schilbe intermedius* Rüppel, 1832, is the oldest available name for fishes previously included in the taxon *S. mystus*. In the present paper, we accept De Vos and Skelton's (1990) nomenclatural changes for the host. It should be recognized, therefore, that the epithet "*Schilbe mystus*" used in previous parasitological literature refers to the species *S. intermedius*, and that "*Eutropius niloticus*" of the older parasitological literature is now referred to *S. mystus*.

Acknowledgments

The authors thank Dr. Mary Beverley-Burton for a presubmission review of the manuscript. The study was supported, in part, by a grant (\$56) from the Faculty Research Committee, Idaho State University.

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